

The Natural History of *Ophioglossum palmatum* in South Florida¹

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Of the sixty or more species in the Ophioglossaceae, only *O. pendulum* L. and *O. palmatum* L. are epiphytes. Although some authors (Chrysler, 1941; Eames, 1936, fig. 78) have regarded these species as relatively primitive in the genus and have envisioned a reduction series culminating in the more diminutive terrestrial species, others have suggested that they are advanced in most respects (Bower, 1911, 1926; Wagner, 1952). Because detailed information about the gametophytes, spore wall sculpturing, stem structure and development, and venation pattern—among other characters—is not available for most species in the genus, strong adherence to either hypothesis serves little purpose at the present time. Nevertheless, the derivative state of the epiphytic habit in *Ophioglossum* is supported by its extremely low frequency of occurrence in the genus and the family and the unique frond architectures displayed by both *O. pendulum* and *O. palmatum*.

Numerous discussions of the peculiar features of these epiphytes, as well as speculations about their evolution, have dominated the literature dealing with them, but little has been reported about their natural history and ecology. For this reason, in this paper I would like to relate observations on the natural history of a population of *O. palmatum*, the Hand Fern, in southern peninsular Florida. In addition, I shall attempt to place these observations into the context of the natural history of *O. palmatum* as it occurs in other parts of its range, as well as that of *O. pendulum* in the Old World tropics.

Ophioglossum pendulum is found throughout the Old World tropics, except for Africa, and is also found in Hawaii (Christensen, 1932; Clausen, 1938, p. 117). It has elongate, ribbon-like blades up to 4 m long and 9 cm wide which often fork in large specimens. Horner (1958), Graf (1970), and Carlquist (1970) each illustrate this species. Each leaf bears one fertile spike which may exceed 50 cm and which is inserted medianly on the sterile portion of the leaf blade. Mature leaf blades are perpendicular to the supporting surface (Wagner, 1952), and stomates are present on both leaf surfaces.

Ophioglossum palmatum is found in the New World tropics, and is also found in South Vietnam, Madagascar, the Seychelles, and Réunion (Christensen, 1932; Tardieu-Blot, 1953; Clausen, 1938, p. 114; Wieffering, 1964). It has blades up to 45 cm long and 30 cm wide which are broad at the base and are divided into a variable number of distal lobes. The leaves of *O. palmatum* have been described as palmately or dichotomously lobed, but no ontogenetic evidence has been presented to support either view. Similarly, the leaf ontogeny of *O. pendulum* is unknown. Craighead (1963) and Troll (1933) illustrate the species. Each leaf bears from one to 15 or more fertile spikes up to 7 cm long which are inserted at the apex

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FIG. 1. *Ophioglossum palmatum* growing from Cabbage Palmetto in Collier County, Florida, $\times \frac{1}{2}$.

of the stipe and along the margin of the blade. Mature leaf blades are parallel to the supporting surface, and stomates are present only on the abaxial surfaces. Contrary to the opinion of Nakai (1925) and figure 78 in Eames (1936, p. 118), the leaves of epiphytic plants of *O. palmatum* are arching or pendent, but not erect, at maturity. Reports of erect leaves are presumably based on rare, terrestrial collections. Both species may rarely occur terrestrially, growing on rotting logs or moss-covered rocks.

Although the two species are generally geographically separate, both have been collected in Madagascar, the Seychelles, and Indochina. Both species have been divided into subspecies or varieties on the basis of leaf size, shape, and texture. These subdivisions are not convincing, however, because intermediate plants occur throughout the range of each species (Clausen, 1938, 1954; Horner, 1958; Wieffering, 1964). A plant resembling *O. palmatum* and perhaps constituting a distinct species has been reported from Zaire (Belgian Congo) by Taton (1944).

A large population of *O. palmatum* located in Collier County, Florida, was investigated in January 1971 and 1972, in March 1972 (dry season), and in July 1973 (wet season). The habitat is a mixed hardwood association bounded on one side by a river and described as a "palmetto hammock" by F. C. Craighead, Sr. (1973, pers. comm.). The dominant trees are Red Maple, Live Oak, Bald Cypress, and the Cabbage Palmetto. The climate is strongly seasonal: 60%–80% of the yearly precipitation falls in a five-month period (May through October), and in some years the monthly rainfall during the dry season may be negligible (Craighead, 1971). During the rainy season the entire area is inundated, but in the dry season most of the ground is exposed. The proximity of the river prevents total drying of the substrate during the dry months, however, and probably accounts for the fact that extensive burning has not occurred in the area in recent years.

At the locality, the Hand Fern was observed growing only on the arborescent Cabbage Palmetto, *Sabal palmetto* (Walt.) Lodd. ex Schultes. The stems of the palm are covered by a mantle of overlapping, fibrous, persistent leaf bases that collect falling debris (Fig. 1). Each leaf base develops a vertical cleft due to expansion forces created by the primary expansion of the trunk (Tomlinson, 1962). Although the trees are at least partially resistant to fire, as indicated by the large numbers of charred but living plants easily observed on a drive through Everglades National Park, the leaf bases are highly flammable. Even without burning, however, older leaf bases gradually decay, loosen, and fall from the trees.

Ophioglossum palmatum lives in the humus that accumulates underneath the leaf bases of the palmettos. Although plants could be observed at various points along the trunks of the palmettos, from near the bases to just below the crown, they are generally restricted to the upper parts of the palmettos. The stem and root system of a particular plant are completely covered and can only be observed after two or three layers of the overlapping, tightly appressed leaf bases have been removed. Mature plants may bear as many as six leaves, all or some of which are fertile. A single leaf commonly produces three to six erect fertile spikes, but larger leaves may bear as many as ten. Although leaves are present on the plants

throughout the year, they are not produced continuously; the peak of leaf development occurs during the summer rainy months, and the sporangia mature between December and May. The fleshy, tuberous stems (1.5+ cm in diameter in older plants) are covered with fine, light brown hairs. Several large, branching roots grow from a stem, radiating for considerable distances under the palmetto leaf-base mantle, in some cases penetrating decaying leaf-base tissues. Rarely, actively growing roots were found attached to inactive, necrotic stems without leaves, and in two instances living roots were found with apparently no stem attachment whatsoever. The succulent character of the roots of the Hand Fern is emphasized by observation of squirrels feeding on them during severe dry weather (W. R. Llewellyn in Craighead, 1963).

Although Small (1938, p. 368) states that in peninsular Florida *O. palmatum* is found "On trees, often among the bases of the leaves of the cabbage tree. . . ," I have been unable to find herbarium sheets or other records documenting its occurrence on any other tree in the state. F. C. Craighead, Sr. and C. E. Delchamps, both of whom have had extensive field experience in southern Florida, report that they have encountered the Hand Fern only on the palmetto.

In other parts of its range, *O. palmatum* is not confined to the Cabbage Palmetto, nor in fact to other palms. Its preference for the Palmetto in southern Florida appears to be the result of the pronounced wet-dry seasonality and the inability of its unprotected sporophytes and gametophytes to withstand xeric epiphytic conditions. The sporophytes are mesophytic. Although the succulent, tuberous stems, roots, and leaves may serve as water reservoirs, there are no obvious structural modifications for rapid uptake of water or for reducing water loss during periods of stress. When sporophytes are removed from the palmettos and left exposed in the air, their leaves begin to wilt almost immediately. Similarly, the slow-growing, parenchymatous gametophytes are highly susceptible to damage by desiccation.

It is not surprising that throughout most of its range *O. palmatum* is confined chiefly to tropical montane sites where moist conditions prevail all year around or with only minor interruption during mild dry seasons (Martens & Galeotti, 1842; Maxon, 1926; Proctor, 1953; Tryon, 1960; W. H. Wagner, Jr. and L. D. Gomez, 1971, pers. comm.; R. G. Stolze, 1973, pers. comm.). Plants of the Hand Fern from these moister regions have most commonly been observed on the branches of various species of dicotyledonous trees, but have also been seen growing on palms, rocks (Martens & Galeotti, 1842), and from the root masses of bromeliads (Wagner, 1974, pers. comm.). The stems and roots of the Hand Fern are embedded in moist humus that accumulates among epiphytic bryophytes, other pteridophytes, orchids, and bromeliads. The requirement for a continuously moist substrate is illustrated by observations of Tryon (1960) in Peru. He noted that when a branch supporting plants of the Hand Fern fell from a tree into a more exposed position, the plants died after a mild dry season.

Specialized epiphytes, such as orchids and tillandsioid bromeliads, are common in southern Florida. But the relatively severe dry seasons characteristic of the area would appear to militate against the occurrence of a mesophytic epiphyte like

O. palmatum. Nevertheless, the Hand Fern was apparently once present at many localities in southern Florida (Small, 1938). The explanation for this appears to lie in the ability of the species to colonize the only microsites that provide a constantly moist substrate; namely, the interfaces between the trunks and persistent leaf bases of the Palmetto. Not all palmettos, however, offer an equally suitable environment. A survey at the Collier County locality indicated that the condition of the leaf base mantle (relatively intact and tightly held versus decayed and loose) determines the moisture content of the humus beneath the leaf bases and, thereby, influences the ability of the Hand Fern to become established. This explains the greater number of Hand Fern plants observed on the upper, younger parts of the Palmettos. Gametophytes occur only in the most moist microsites, but the sporophytes are slightly more tolerant of drier conditions. Plants were never observed, however, on exposed trunks which had fallen leaf bases or which had been damaged by fire.

The Hand Fern has disappeared from many of its previous localities in southern Florida (Small, 1938) and now is perhaps in danger of extinction there. In a letter to M. A. Chrysler (Chrysler, 1941), J. K. Small wrote "Forty or fifty years ago one could go to the edge of the Everglades back of Miami and collect it by the wagon load. Today not a leaf can be found there." Part of the explanation for the disappearance of the species from southern Florida has been extermination of colonies by collectors. For example, Dr. Craighead (1973, pers. comm.) reports that prior to the opening of Mahogany Hammock (Everglades National Park) to the public, as many as 40 to 50 Cabbage Palmettos bore plants of the Hand Fern. Subsequently, "Most of the orchids were soon removed by collectors and finally the Hand Fern. I then searched the entire hammock and did not find a single Hand Fern plant. Later, several more surveys were made with the same results." The superficial resemblance of the Hand Fern to *Platycerium* has earned for it the additional local name of "Dwarf Staghorn" and accounts for collections by those seeking to grow it in cultivation. The species, however, has not had even the limited success in cultivation as that enjoyed by *O. pendulum* (see Graf, 1970).

More important than the effects of over-collection in understanding the decline of *O. palmatum* are the recent extensive drainage and water diversion activities in the Everglades. These programs have had the effect of prolonging the dry season to the extent that soils that previously remained moist until the onset of the summer rains were allowed to dry. The result has been a marked increase in the frequency and severity of fires (Craighead, 1971, 1973). Fires destroy the leaf bases of the Palmettos and thereby the only available habitat for the Hand Fern in the area. Thus, *O. palmatum* persists today only in moist hammocks that have escaped fire (Craighead, 1963).

More is known about the natural history of *Ophioglossum pendulum* than of *O. palmatum*, perhaps because it is more common through its range and is a more conspicuous element of the vegetation. The species is confined to moist tropical regions (lowlands or montane) characterized by an almost even distribution of rainfall throughout the year. Short "dry" seasons do occur, however, as well as daily fluctuations in the amount of rainfall input and humidity (Walter, 1971). For example, although at Tjibodas (Java) in some years there may be as many as 300

rainy days, rarely are there three weeks without rain (Went, 1940). In addition, humidity decreases at higher levels in the forest, falling as low as 40% at 18 m (Schimper & Faber, 1935). Consequently, the mesophytic epiphyte *O. pendulum*, often growing in open forests, must rely on a humus substrate that acts as a water reservoir and buffer against desiccation as well as a source of nutrients.

Holttum (1954a, p. 41) reports that in the lowlands of Malaya, *O. pendulum* "is sometimes found on tree trunks where humus has collected, but more often on palms which have persistent leaf-bases." Wagner and Grether (1948a) observed small plants growing in moss at the bases of Sago Palms in the freshwater swamps of the Admiralty Islands. At high elevations (1000–1500 m) in the Philippines, plants grow "in the root masses of *Asplenium cymbifolium* Christ and also from sheltered crevices in mossy trunks and branches from mats of bryophytes and Hymenophyllaceae." (M. G. Price, 1974, pers. comm.). *Ophioglossum pendulum* has perhaps most often been observed growing from the accumulation of humus at the bases of plants of *Asplenium nidus* and *Platycterium* spp. (Holttum, 1954a,b; Wagner & Grether, 1948a,b; Wieffering, 1964; M. G. Price, 1974, pers. comm., Went, 1940; Campbell, 1907). Holttum (1938) suggests that hardy epiphytes like *Asplenium nidus* and *Platycterium coronaria* colonize relatively exposed, xeric positions in the canopy and make possible subsequent growth of mesophytic epiphytes like *O. pendulum*. Larger plants of *O. pendulum* compete with *Platycterium* plants for nutrients and moisture and in this way may eventually kill the *Platycterium* (Holttum, 1954b). Campbell (1907, p. 140) observed in Ceylon that "*O. pendulum* was found to be fairly abundant near Hanwella, but the weather was very dry, so that the masses of humus in which the plants were growing were dry as powder and no prothallia could be procured." This observation suggests that as with *O. palmatum*, the gametophytes of *O. pendulum* are less resistant to dry conditions than the sporophytes.

Both *Ophioglossum palmatum* and *O. pendulum* are relatively unspecialized, mesophytic epiphytes. Both species require a more or less constantly moist humus substrate for establishment and maintenance of growth. Under conditions of relative drought, such as the seasonal climate of southern Florida or close to the canopy in the Malayan evergreen forest, plants are restricted to microsites with humus masses protected against desiccation. In Florida, it is the leaf-base mantle of the Cabbage Palmetto that affords the necessary protection, while in Malaya it is often the bases of nest or bracket epiphytes. In addition to providing moisture and nutrients, the humus provides a substrate for the endophytic fungus essential to the growth of the gametophytes and young sporophytes and satisfies the probable dark requirement for spore germination (see Whittier, 1973).

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